A Numerical Taxonomic Study of Hawaiian Reef Corals[1]

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ABSTRACT: Sixty characters were measured and used in multivariate statistical programs to study the systematics of 20 species of Hawaiian corals. Correlation and distance phenograms and a computer-generated, three-dimensional model were used to develop phenetic rankings of species groups at levels corresponding to the taxonomic categories of genus, family, and, provisionally, suborders.

THE SCLERACTINIA is an order of the Coelenterata. These stony corals have one of the better invertebrate fossil records. Numerous attempts have been made to classify them by various criteria, ranging from gross anatomy to physiology. In the literature, the different classifications seem to be almost as numerous as the species being classified (Hyman, 1940; Bourradaile and Potts, 1963; Dana, 1890; Duerden, 1904; Hickson, 1924; Fowler, 1885–1889; Ogilvie, 1896; Robinson, 1923; Vaughan and Wells, 1943). Consequently, there is no general agreement on the systematics of the order. The controversies arise because various authors have chosen different characters to emphasize in their classifications. The effects of such emphases can be minimized by measuring a large number of kinds of characters and treating them in statistical programs that preclude inadvertent weightings. This procedure was used to classify 20 species of scleractinian corals and to compare the results with prior classifications in an effort to help stabilize the taxonomy (systematics) of the order.

MATERIALS AND METHODS

All corals studied were collected from the waters around the island of Oahu, Hawaii; most were taken from Kaneohe Bay in the summer of 1967. All species except *Cyphastrea ocellina* and *Pocillopora ligulata* were found in samples from several different reefs. *Tubastrea aurea* was obtained from a patch reef within the bay and from a sunken ledge outside the bay.

All observations on soft, live parts were made either on living corals at the University of Hawaii Institute of Marine Biology or from colored photographs taken there.

Twenty species, referred to as operational taxonomic units (OTU's) (Sokal and Sneath, 1963), were collected, and 60 characters (listed below) were measured for each. Qualitative characters were rated 1.0 if the character was present and 0.0 if the character was lacking. All quantitative characters were measured between 50 and 100 times. The mean was used as the value of the character measured. If there was greater variation within an OTU than between the means of different OTU's, the character was discarded as insignificant. Table 1 lists the species by the randomly assigned code numbers, which were used to reduce subjectivity when recording the values of the characters. Ideally, the author should neither assign the code numbers nor see the code key until he has finished the analysis.

CHARACTERS MEASURED

1. Septa present or absent.
2. If septa present, degree of septal development.
3. Septa margins: beaded, dentate or smooth.
4. Are septa fenestrate?
5. Secondary septa present or absent.
6. Tertiary septa present or absent.
7. Quaternary septa present or absent.
8. Are directive mesenteries present or absent?
9. Are septa costate?
10. Corallite walls present or absent.
11. Zooxanthellae present or absent.
12. Exotheca present or absent.
13. Endotheca present or absent.
14. Peritheca present or absent.
15. Pali present or absent.
16. Snapticulae present or absent.
17. Collines present or absent.
18. If septa are fenestrate are they laminar in later stages?

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TABLE 1

CODE NUMBER	GENUS AND SPECIES
1	*Pocillopora ligulata*
2	*Montipora verrilli*
3	*Psammocora stellata*
4	*Porites evermanni*
5	*Pavona explanulata*
6	*Fungia patella*
7	*Cyphastrea ocellina*
8	*Pocillopora meandrina*
9	*Montipora verrucosa*
10	*Porites compressa*
11	*Fungia scutaria*
12	*Leptastrea bottae*
13	*Tubastrea aurea*
14	*Pocillopora damicornis*
15	*Montipora patula*
16	*Psammocora verrilli*
17	*Porites lobata*
18	*Pavona varians*
19	*Fungia fragilis*
20	*Leptastrea purpurea*

19. If peritheca present is it porous or nonporous?
20. Is stomodaeum smooth or rough?
21. Is sphincter well developed?
22. Nematocysts per tentacle (many or few)?
23. If corallite walls are present are they porous or nonporous?
24. If colonial, are the coelentera intercommunicating by a basal canal system?
25. Is primary pigmentation carotinoid?
26. Intra- or extratentacular budding.
27. Are calices above general surface of coral?
28. Is coral colonial or solitary?
29. Is columella developed?
30. If columella developed is it low-boss or absent?
31. If columella developed is it styloid or laminar?
32. Trabeculae, many or few.
33. Trabecular inclination from axis of divergence (Vaughan and Wells, 1943).
34. Epitheca present or absent.
35. Septa or peritheca present or absent.
36. Is snaptotheca present or absent?
37. Is corallum cercoid?
38. Is corallum plocoid?
39. Is corallum meandroid?
40. Is corallum montiporoid?
41. Is corallum thamnestroid?
42. If montiporoid, is it explanulate?
43. If plocoid is it glomerate?
44. Mural denticles present or absent.
45. Found mostly on windward or leeward side of reef?
46. Found in sunny or dark areas?
47. Relative dominance on reefs.
48. Is corallum generally porous or nonporus?
49. Number dead colonies per 100 ft of reef frontage.
50. Average bathymetric range.
51. Average height of calyx.
52. Average height of dentitions or beads.
53. Distance between calices.
54. Average annual increase of length (Edmondson, 1929; Tamura and Hada, 1932; Stephenson and Stephenson, 1933).
55. Average percent of weight increase (Ref. same as above).
56. Glucose-6-phosphate dehydrogenase activity (Powers, Lenhoff, and Leone, 1968).
57. 6-Phosphogluconate dehydrogenase activity (Powers, Lenhoff, and Leone, 1968).
58. Ratio between length and width of calyx.
59. Number of calices per unit area.
60. Ratio of height to width of calyx.

After the values of the characters were recorded for each OTU, these data were punched onto IBM cards for processing in a G.E. 625 digital computer. The group of programs used were from *NT-SYS Numerical Taxonomy System of Multivariate Statistical Programs* (Rohlf et al., 1967). The data were standardized by characters. Correlation and distance coefficients were computed for each pair of species, based on the standardized data. Because the coefficients measure different aspects of phenetic similarity, both methods were used (Rohlf and Sokal, 1965; Rohlf et al., 1967). After the entire correlation and all distance matrices had been calculated, a clustering analysis program was used to do an unweighted pair group method of arithmetic averages (UPGMA) to summerize the information contained in the 20 $\times$ 20 matrices. The program also generated "phenograms" (Figs. 1 and 2) and cophenetic value matrices. Another program was used to compare the correlation and distance matrices with their respective cophenetic value matrices (see correlation at bottom of Figs. 1 and 2). Another program calculated the eigenvalues and eigenvectors of the 60 $\times$ 60 matrix of correlations among the characters, using the Jocobi method (Rohlf et al., 1967). The 20 OTU's were then projected onto the first three eigenvectors.

Another program computed the shortest, simply connected network through the series of 20 points (OTU's), computed a perspective view of a three-dimensional scatter diagram, and prepared a magnetic tape for a B.L. plotter, which was used to prepare Figure 3.

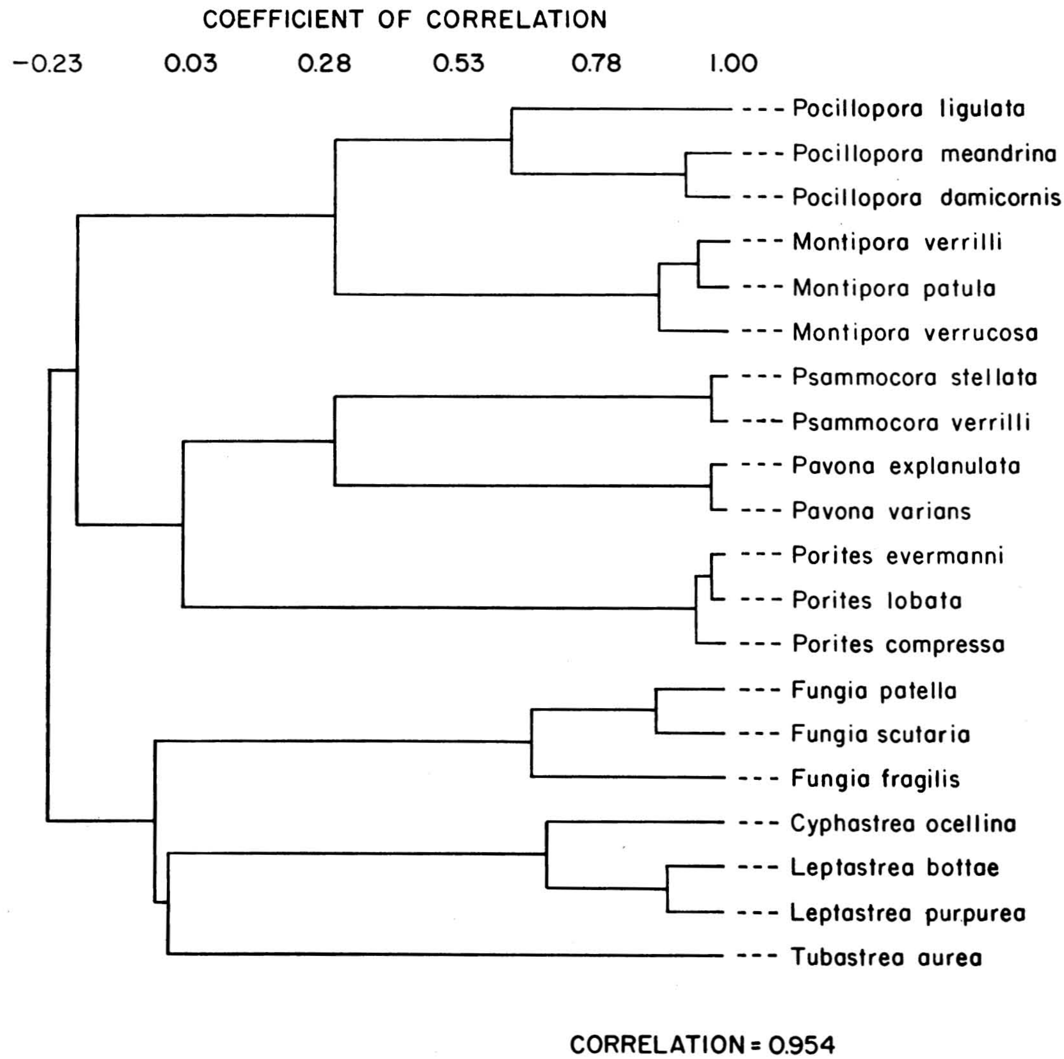

FIG. 1. A computer printed coefficient of correlation phenogram. The correlation between the original correlation matrix and the cophenetic value matrix is below the phenogram.

RESULTS AND CONCLUSIONS

Hawaii is in the northern region of the lush coral growth zone. The islands are in the central Pacific and have a coral fauna most like that of Japan and the tropical Pacific islands. A few species, however, are common to the Panamanian area. There are only 52 species from 14 genera present in the Hawaiian group (Vaughan and Wells, 1943), and the present study has sampled 9 of these genera. Vaughan and Well's classification of the Hawaiian corals is given below. As will be seen, my data strongly support this classification.

CLASSIFICATION ACCORDING TO VAUGHAN AND WELLS (1943)

Class: ANTHOZOA Ehrenberg, 1843
Order: SCLERACTINIA Bourne, 1900
Suborder: ASTROCOENIIDA Vaughan and Wells, 1943
Family: ACROPORIDAE Verrill, 1902
1. *Montipora verrilli*
2. *Montipora patula*
3. *Montipora verrucosa*
Family: SERIATOPORIDAE Milne-Edwards and Haime, 1849
4. *Pocillopora ligulata*
5. *Pocillopora meandrina*
6. *Pocillopora damicornis*

Suborder: FUNGIIDA Duncan, 1884
Family: THAMNASTERIIDAE Vaughan and Wells, 1943
7. *Psammacora stellata*
8. *Psammacora verrilli*
Family: AGARICIIDAE Gray, 1847
9. *Pavona explanulata*
10. *Pavona varians*
Family: PORITIDAE Gray, 1842
11. *Porites evermanni*
12. *Porites lobata*
13. *Porites compressa*
Family: FUNGIIDAE Dana, 1848
14. *Fungia patella*
15. *Fungia scutaria*
16. *Fungia fragilis*

Suborder: FAVIIDA Vaughan and Wells, 1943
Family: FAVIIDAE Gregory, 1900
Subfamily: MONTASTREINAE Vaughan and Wells, 1943
17. *Leptastrea bottae*
18. *Leptastrea purpurea*
19. *Cyphastrea ocellina*

Suborder: DENDROPHYLLIIDA Vaughan and Wells, 1943
Family: DENDROPHYLLIIDAE Gray, 1847
20. *Tubastrea aurea*

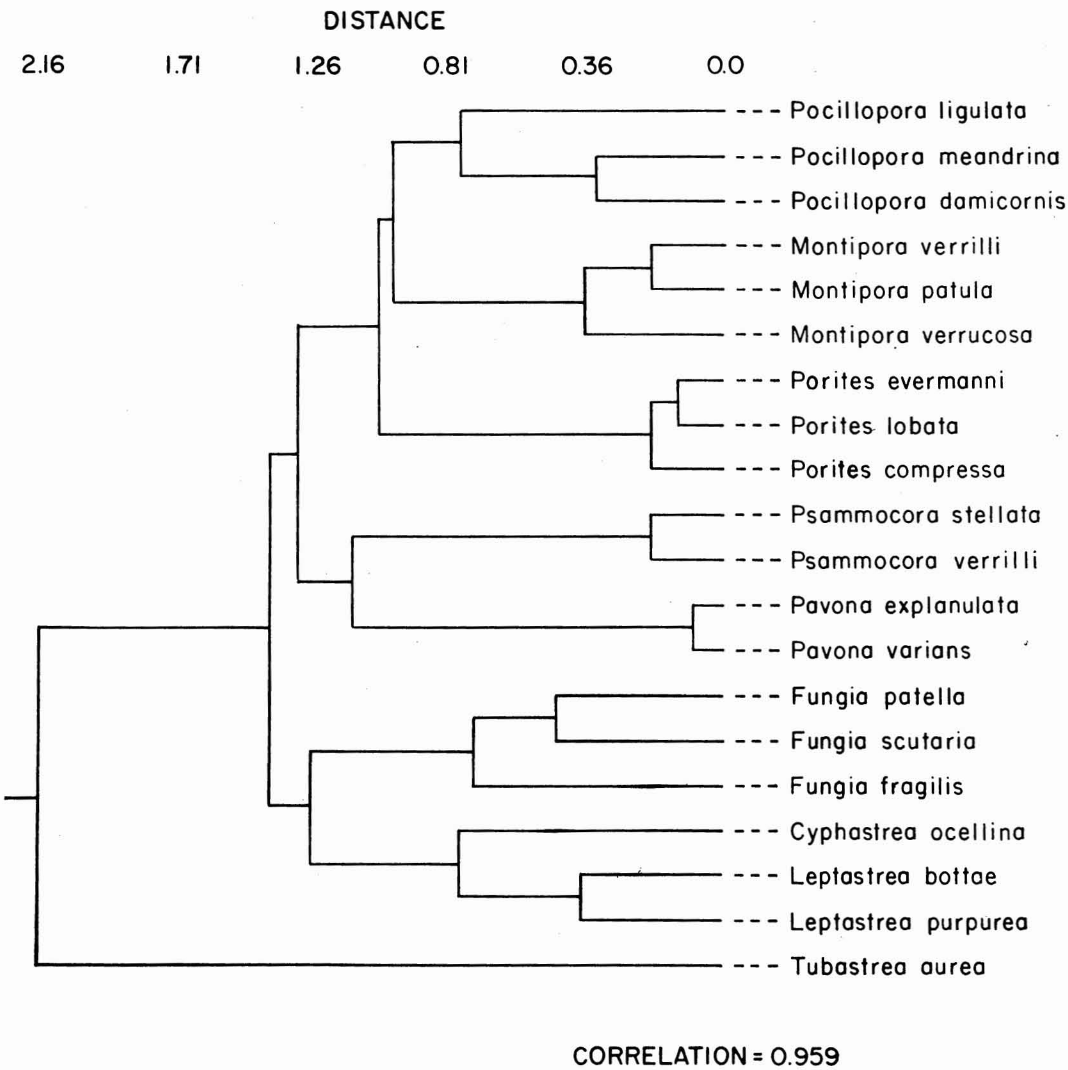

FIG. 2. A computer printed distance phenogram. The correlation between the original distance matrix and the cophenetic value matrix is below the phenogram.

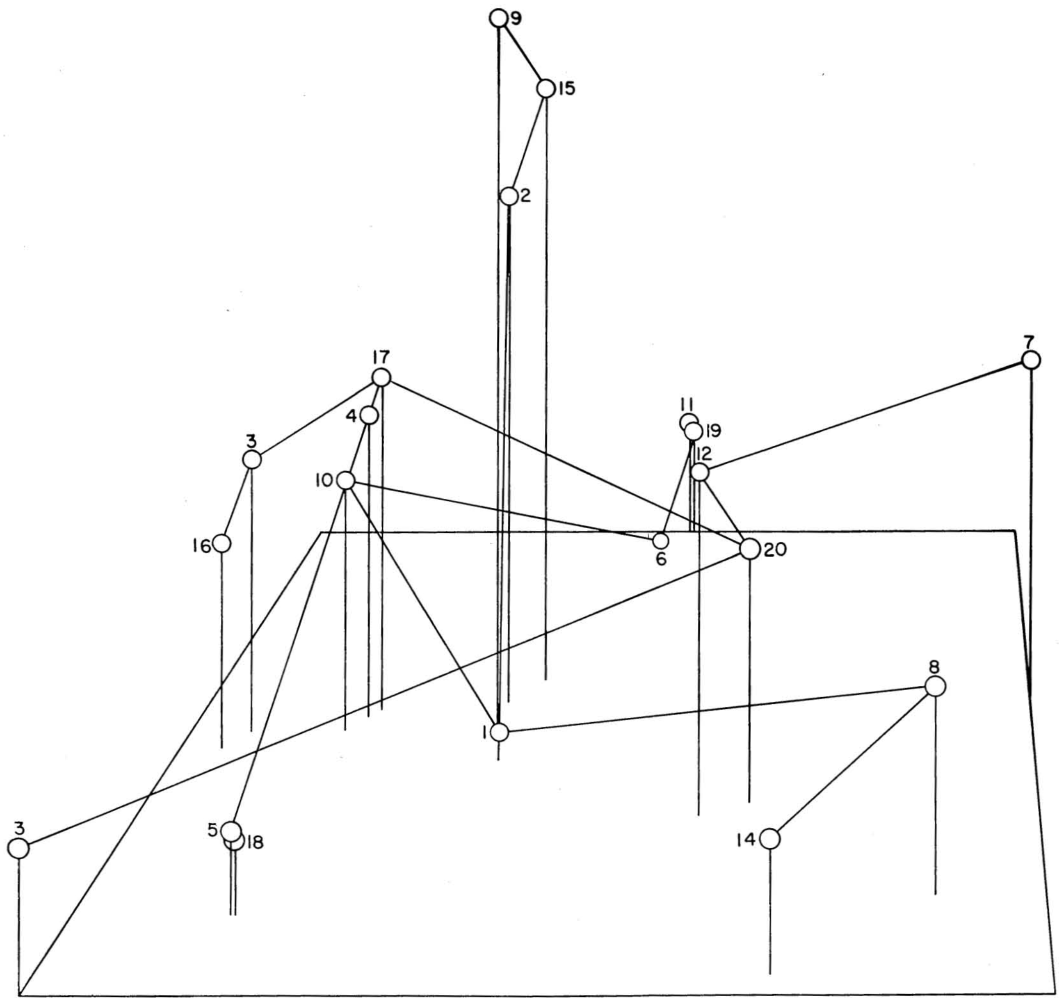

FIG. 3. Perspective 3-D model of species. The numbered balls are the coded species. Lines connect each species with the next closest species. Vertical lines indicate the position of the species with respect to the base of the model.

The phenogram in Figure 1 summarizes the relationships given by the correlation matrix. The correlation between the phenogram and the original 20 $\times$ 20 matrix is 0.954. Therefore, the phenogram is an excellent representation of the original matrix. Although it resembles one, this phenogram should *not* be confused with a phylogenetic tree. Obviously, Figure 1 shows that members of the same genera are grouped fairly tightly together. It is noteworthy, however, that *Pocillopora ligulata* appears to be phenetically more different from members of this genus than other species are from members of their genera. In addition, *Fungia fragilis* shows a slight phenetic uniqueness. *Cyphastrea* is clustered with the two *Leptastrea* species, which is not surprising because these genera are considered to be in the same family (Vaughan and Wells, 1943). Furthermore, all the pocilloporans are clustered at lower correlations with the montiporans. The psammocorans and pavonans are definitely clustered together. All other linkages are at such levels that their phenetic affinities are ignored at this time. If the number of species being compared were greatly increased, the linkage groups with greater coefficient values probably would not be affected, but the lower linkage groups (clustered at low values) would probably change. Therefore, the lower linkage groupings should be accepted with caution until a more comprehensive study, including a better and broader representation of genera, can be made.

The phenogram in Figure 2 summarizes the data found in the distance matrix. The correlation is 0.959, and so the phenogram is highly representative of the matrix. The results are similar to those of the preceding section. Species in each genus and family are clustered together. The distinction between *Tubastrea aurea* and the rest of the corals is sharper than in the correlation phenogram. The arrangement of the other groups, however, is much less certain. Undoubtedly, several of the distant clusters are real, but it is difficult to decide which groupings are important and which are artifacts resulting from the small number of genera represented.

The computer-generated, three-dimension model (Fig. 3) provides more information on the phenetic interrelations of the larger clusters of species, that is, those grouped at a distance value of 1.26 and larger, in Figure 2, and a correlation coefficient of 0.28 and smaller, in Figure 1. The model shows the members of the same genera grouped close together with the exception of *Pocillopora ligulata* (code number 1), which is far enough away from the other pocilloporans to suggest that it may be considered as another genus in the family Seriatoporidae. The position of *Pocillopora ligulata* in the drawing explains why the *Porites* group has lesser affinity to *Pocillopora* although the group is actually much closer to the mean position of *Psammocora, Pavona* or *Fungia* than to the mean position of *Pocillopora.* Consequently, until more evidence from an expanded study is available, the slight affinity of *Porites* to *Pocillopora* should be considered doubtful, and due simply to the presence of the unusual member *Pocillopora ligulata.*

Figure 3 reaffirms the uniqueness of *Tubastrea.* There is a suggestion of weaker affinities among *Porites, Psammocora* and *Pavona. Fungia* either is phenetically unique or has a weak affinity for *Porites.* The model reaffirms the affinity of *Cyphastrea* to the two *Leptastrea* species. Despite the small number of genera represented, the groupings shown in Figure 3 are an accurate representation of the data from 60 characters. The suggested larger clusters correspond to the suborders of Vaughan and Wells. However, Figure 3 also suggests that the clusters above the genus level are not spherical, which would account for phenogram irregularities. An expanded study is in progress to test this hypothesis.

SUMMARY

1. The numerical taxonomic study grouped members of the same genera and families together.

2. The groupings provisionally suggest the subordinal classification adopted by Vaughan and Wells (1943).

3. These data conform more closely to the classification of scleractinian corals provided by Vaughan and Wells than to others that have been proposed.

4. Numerical taxonomic methods are indicated to be extremely useful adjuncts in scleractinian systematics.

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